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Pliocene taxodiaceous fossil wood from southwestern Ukraine and its palaeoenvironmental implications

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Abstract Mineralized wood collected from Late Pliocene strata near Gorbki village in the Transcarpathian region of Beregovo Kholmogor′e in southwestern Ukraine was anatomically studied and identified. The wood possesses distinctive anatomical features and has distinct growth rings with an abrupt transition from early- to late-wood. Wood consists of tracheids with 1−3 seriate, dominating bi-seriate, opposite pits on the radial walls and taxodioid cross-field pitting, indentures present. Rays are uni-seriate and 1 to 73 cells high. Ray parenchyma horizontal walls thin and smooth. Axial parenchyma distributed in early- and late-wood and is solitary and diffuse, with end walls nearly smooth or slightly nodular. The combination of features observed in the wood indicates it belongs to the conifer family Taxodiaceae and is most similar to modern *Sequoia* and assigned to the fossil genus *Sequoioxylon*. Comparison with species of *Sequoioxylon* show it is most similar to *Sequoioxylon burejense*, but ray tracheids were not found in our specimens. We describe the specimens here as *Sequoioxylon* cf. s. *burejense* noting this similarity. Extant *Sequoia* is distributed in the northern California coastal forest eco-region of northern California and southern Oregon in the United States where they usually grow in a unique environment with heavy seasonal precipitation (2500 mm annually), cool coastal air and fog drip. This study supplies magafossil evidence of *Sequoioxylon* as an element of the Late Pliocene forest community in Ukraine and indicates a climate with heavy seasonal precipitation and fog drip.

Key words Late Pliocene, gymnosperm, conifer, *Sequoioxylon*, fossil wood, Ukraine

1 Introduction

Identification of tree species based on wood anatomy is of interest not only to taxonomists studying extant vegetation, but also for studies focusing on past environments and ecosystems especially when other vegetative and reproductive parts of fossil plants are not available. The conifer family Taxodiaceae were widespread in recent geological history where for instance they were often the dominant floristic component such as in lowland swamp forests of North America, Europe and Asia during the Late Cretaceous and into the Middle Tertiary (Chaney, 1951; Florin, 1963). The Taxodiaceae then declined and ultimately disappeared from Europe during the Pliocene and Early Pleistocene (Michaux *et al*., 1979). Extant members of the Taxodiaceae belong to nine genera that encompass 12 species which are distributed in East Asia and North America; one genus, *Athrotaxis*, is found in Tasmania within Australasia (Wu and Raven, 1999). In this paper we

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describe a taxodiaceous species based on a specimen of mineralized wood from the Late Pliocene sediments of the Ilnitsa Suite of southwestern Ukraine.

2 Material and methods

2.1 Material

The fossil specimen was collected from the Gorbki brown coal field by Professor Vladimir Syabryaj. The locality is near Gorbki village in the Transcarpathian region of Beregovo Kholmogor′e in southwestern Ukraine (Fig. 1). The coal-bearing sediments belong to the Ilnitsa Suite which consists of alternating aleurolites, coaly clays, tuffites and coal beds. According to faunal data (Sheremeta, 1958), pollen and spore community and composition (Syabryaj, 1997) and the stratigraphical scheme of the Central Paratethys, the age of the Ilnitsa Suite is Late Pliocene. The coal-bearing sediments contain five coal layers. The Ilnitsa section is the most complete succession regionally and comprises five coal layers. However, the Gorbki brown coal field section contains only the upper three coal layers. The studied fossil was collected from the roof of the second coal seam (Fig. 2). Part of the material is solid and permineralized to facilitate anatomical preservation while some parts of the specimen are more fibrous and hair-like due to the separated cell strands that represent petrified tracheids (Fig. 3).

2.2 Methods

The separated parts of the specimen were extracted directly and either mounted using Canada Balsam for examination by light microscope or mounted on stubs to be studied by Scanning Electron Microscopy (SEM). In addition, ground petrological thin sections were made by standard techniques. The fine preserved structures show anatomical details of the original plant tissues. The original pieces (P. U−001) and thin sections of the fossil are deposited in the National Museum of Plant History of China, Institute of Botany, Chinese Academy of Science, Beijing. Anatomical analyses were performed with a light microscope and described using the terminology of Richter *et al*. (2004) for softwood identification wherever possible. Mean and maximum numbers of cells were determined from 50 replicates for each character measurement.

Since accurate identification of fossil wood requires detailed descriptions and comparisons with well-described extant wood, preferably from vouchered specimens (Visscher and Jagels, 2003), the fossil wood was compared with published literature and sections of modern material housed in the Wood Herbarium, Research Institute of Wood Industry, Beijing, China. Finally, the specimen was

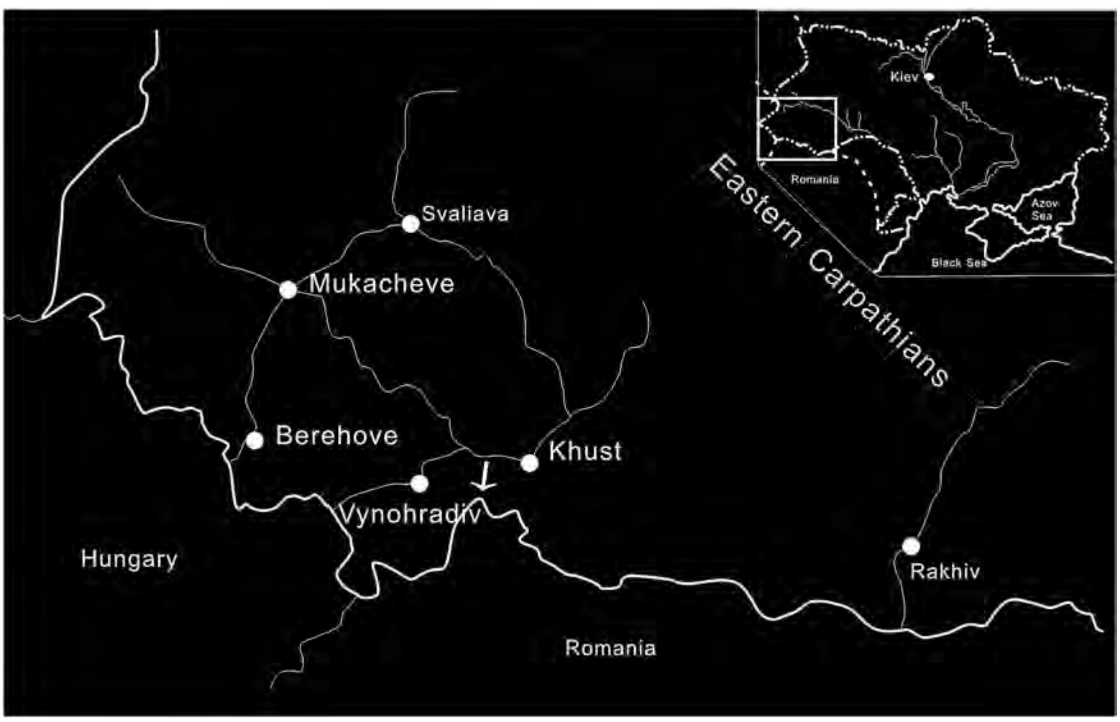

Fig. 1 Map showing the fossil locality (marked with arrow).

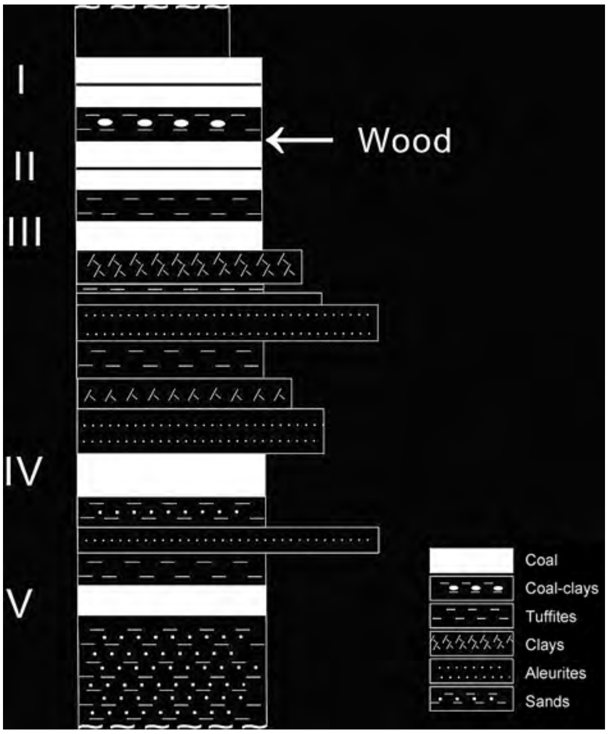

Fig. 2 A partial section of the Ilnitsa section showing fossil wood horizon.

compared with similar fossils formerly assigned to the Taxodiaceae.

3 Systematic description

Family: Taxodioceae, Warming

Genus: *Sequoioxylon* Torrey, 1923

Type species: *Sequoioxylon montanense* Torrey, 1923

Species: *Sequoioxylon* cf. s. *burejense* Blokhinaa, Afonina, and Kodrul, 2010

The description of the wood is based on the anatomical characteristics of a piece of mineralized secondary xylem, 6–8 cm in thickness and 15 cm in length.

The secondary xylem is homogeneous. The growth rings are distinct and of variable width. The transition from early- to late-wood is abrupt (Fig. 4A–4C); a distinct change of tracheid wall thickness between early– and late-wood can be observed in which latewood is narrow or wide. False rings are observed (Fig. 4B). Early-wood tracheids range from 39–78 μm (mean 56 μm, s.d. 9.4) in radial diameter and 30–70 μm (mean 54 μm, s.d. 8.8) in tangential diameter; thickness of cell walls varies from

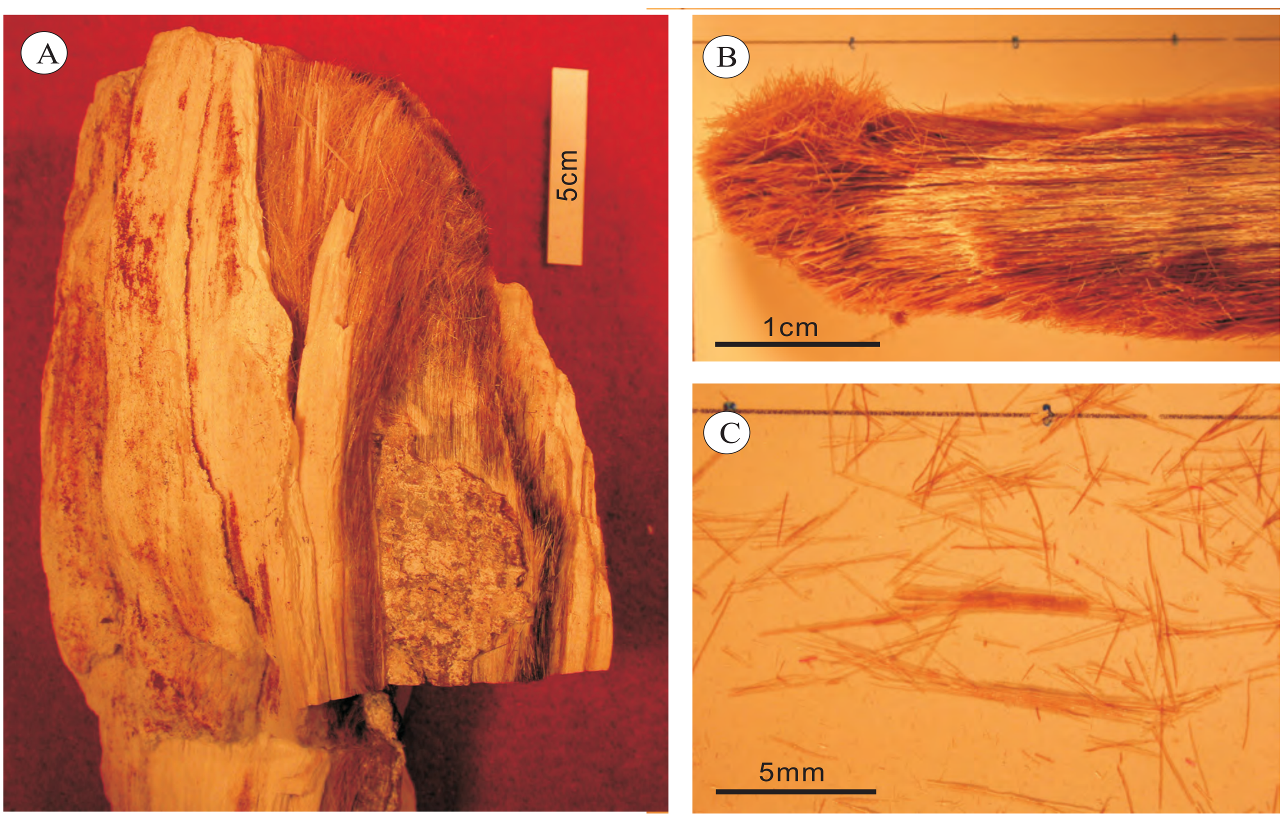

Fig. 3 Fossil wood appearance. A–External features of the fossil wood specimen. B–C–Separate silicified tracheids (see materials and methods for description).

2.2−4.3 μm; outline is distinctly polygonal, rectangular to squarish in cross section (Fig. 4A). Late-wood tracheids vary from 12−35 μm (mean 21 μm, s.d. 6.1) in radial diameter and 28−36 μm (mean 33 μm, s.d. 2.1) in tangential diameter; thickness of cell walls varies from 3.4−8.2 μm; outline is squarish, oblong, or rectangular in cross section (Fig. 4C). Outline of tracheid ends is regular or irregular (Fig. 4H).

Bordered pits on radial walls of tracheids are uniseriate, biseriate (Fig. 4I−4J), and occasionally tri-seriate (Fig. 4K), opposite, circular and partly elliptical; diameter of pits is about 16−34 um. A torus is presents (Fig. 4G). Pits with notched borders are present (Fig. 4N) and crassulaes are consistently observed (Fig. 4J−4K). Tracheids are distinctly pitted on the tangential walls. Pits are circular bordered, and apertures are lentoid (Fig. 4F).

Rays are homogeneous, mostly uni-seriate (Fig. 4D), partly bi-seriate (Fig. 4H) with bi-seriate ranges which are 1−11 cells long (Fig. 4G), or 1−3 paired pits present in a single ray. Ray are from 1 to 73 cells high (up to 1.33 mm) and commonly over 30 cells high. Ray cells are 13−36 μm (mean 19 μm, s.d. 5.1) high and 11−20 μm (mean 15 μm, s.d. 2.7) wide in tangential section. End walls of ray parenchyma cells are smooth (Fig. 4P), vertical or oblique. Horizontal walls of ray parenchyma cells are smooth to sparsely pitted, about 2.3−4.8 μm (mean 3.7 μm, s.d. 0.8) thick. Indentures are present in some end walls of ray parenchyma cells (Fig. 4P). Ray tracheids are not observed.

One to six taxodioid pits are present per cross-field (Fig. 4L, 4Q), and occur in one to five pits in one horizontal row or one to three pits in two or three horizontal rows. Cross field pits are 8.8−15.8 μm (mean 12 μm, s.d. 0.9) in horizontal diameter and broadly elliptical; apertures are horizontal or oblique; some pits have a narrow margin. Sometimes pit size is different in one cross window, and the arrangement is slightly irregular.

Axial parenchyma is present in both early- and late-wood but not abundant, and it is solitary and diffuse, and usually filled with dark-brown contents (Fig. 4A, 4C). Transverse end walls are nearly smooth or slightly nodular (Fig. 4E).

Normal resin canals are absent while axial traumatic resin canals are present (Fig. 4B).

4 Discussion

4.1 Comparison with modern wood

The combination of distinct growth rings, smooth to sparsely pitted horizontal and tangential walls of ray parenchyma, rays from 1−70 cells high, and 1−6 dominantly taxodioid pits in the cross-fields, in association with the absence of normal resin ducts and spiral thickening, indicates that the studied wood belongs to taxodiaceous secondary xylem (Phillips, 1949; Greguss, 1955).

Species of taxodiaceous wood are difficult to distinguish from each other because of their overlapping characters (*e.g.*, Basinger, 1981; Fairon-Demaret *et al*., 2003). Furthermore, there are different opinions about the diagnostic value of these characters. Usually the determination of taxodiaceous fossil or extant secondary xylem relies heavily on the cross-field pits (Peirce, 1936; Kräusel, 1949) and the morphology of the horizontal wall of the secondary xylem parenchyma cells (Greguss, 1955). Among the extant members of Taxodiaceae, viz., *Athrotaxis*, *Cryptomer*ia, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron* and *Taxodium*, the present fossil shows many similarities to the wood structure of *Cryptomeria* and *Cunninghamia* according to Pierce′s (1936) key or *Sequoia* (include *Sequoiadendron*), *Metasequoia*, *Cryptomeria*, and *Cunninghamia* according to Greguss′ (1955) key. Pits with notched borders have been observed only in a few species in particular genera. Due to its restricted occurrence this character appears to be of considerable diagnostic value for identification purposes. Within the Taxodiaceae pits with notched borders occur in *Athrotaxis cupressoid*es, *Athrotaxis selaginoides*, *Cryptomeria* and *Sequoia* (Willebrand, 1995). The presence of pits with notched borders, the abrupt transition from early− to late-wood, and 1−3 seriate pits on radial walls of tracheids in the studied wood indicates a structure most similar to *Sequoia* rather than with *Sequoiadendron*, *Metasequoia*, *Cryptomeria* and *Cunninghamia*.

4.2 Comparison with fossil wood

Wood of many taxodiaceous species of Late Mesozoic and Tertiary age have been assigned to *Taxodioxylon* Geoppert, *Sequoioxylon* Torrey, *Metasequoioxylon* Greguss, *Taiwanioxylon* Chudajb and *Glyptostroboxylon* Conwentz or have been assigned to an extant genus within the family Taxodiaceae.

Torrey (1923) proposed the formal genus *Sequoioxylon* for fossil woods of the Taxodiaceae with traumatic resin canals. Kräusel (1949) analyzed fossil woods of the Taxodiaceae and recommended the use of *Sequoioxylon* only for un-doubtful fossil woods of Sequoieae, and assigned all other woods of Cretaceous and Cenozoic Taxodiaceae to the formal genus *Taxodioxylon* Hartig emend. Gothan

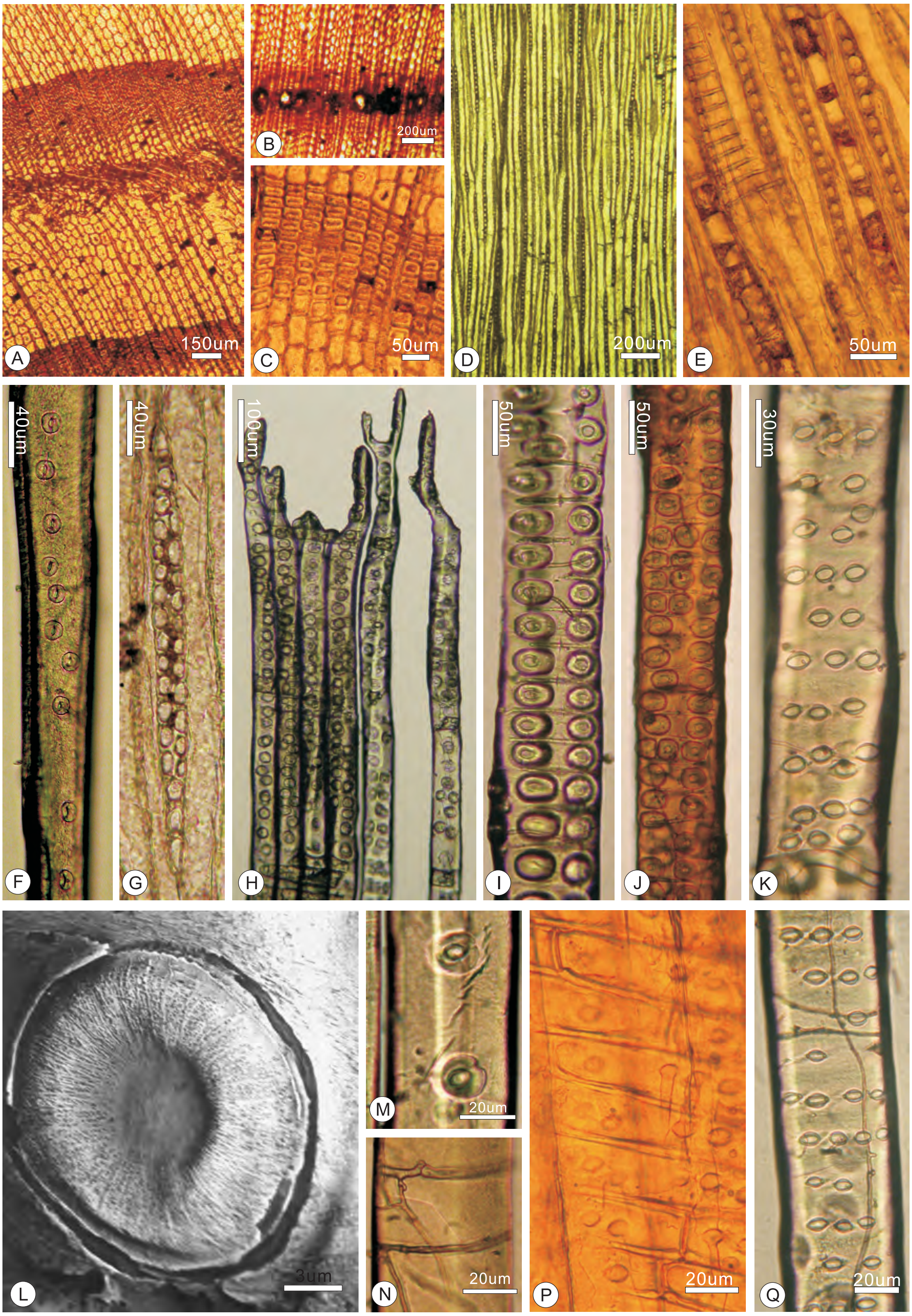

Fig. 4 Anatomical features. A−Transverse section, showing distinct growth rings; B−Transverse section showing axial traumatic resin canals; C−Transverse section showing abrupt transition from early- to late-wood; D−Tangential section showing uni-seriate rays; E−Tangential section showing axial parenchyma; F−Tangential section showing small pits on tracheid tangential wall; G−Tangential section showing bi-seriate ray; H−Tracheids end; I−Bi-seriate pits and crassulaes; J−Occasional tri-seriate pits on tracheid radial wall; K−Taxodioid cross-field pits; L−Torus observed under scanning electron microscopy; M−Notched border pit; N−Fungal hyphae in tracheid; P−Indentures present on ray parenchyma end wall; Q−Taxodioid cross-field pits.

(Gothan, 1905). Therefore, *Taxodioxylon* unites fossil wood showing anatomical characters similar to those in wood of the modern *Sequoia*, *Sequoiadendron*, *Metasequoia*, *Taxodium* and *Athrotaxis*. Schönfeld (1955), Süss and Velitzelos (1997), and some other authors assign all taxodiaceous woods to the genus *Taxodioxylon*. However, Greguss (1967), Basinger (1981), Blokhina (1986, 1997, 2004), Blokhina and Nassichuk (2000), and Iamandei and Iamandei (1999) used the formal genus *Sequoioxylon* for fossil wood showing anatomical characters of the modern representatives of Sequoieae.

Until now, various types of fossil wood with anatomical features of *Sequoia* have been described from Cretaceous to Cenozoic deposits, including *Sequoioxylon chemrylicum* Blokh. (Blokhina, 1997) from the Paleocene−Lower Eocene of the Chemryl Cape, North Western Kamchatka Peninsula, *Sequoioxylon sachalinicum* Blokh. (Blokhina, 2004) from the Paleocene−Eocene of Agnevo River, Alexandrovsk District, and Lower Eocene of Avgustovka River, Uglegorsk District, Sakhalin, *Sequoioxylon sizimanicum* Blokh. (Blokhina, 1986) from the Upper Oligocene of Siziman Bay, Khabarovsk Region, and *Sequoioxylon burejense* from the Upper Cretaceous of the Zeya Bureya Basin of Amur Region, Russian Far East (Blokhina, 2010). Compared with these species of *Sequoioxylon*, in the present species the occurrence of usually high rays, frequent presence of pits with notched borders, distinct indenture in ray cells, 1−5 pits in a single horizontal row and axial traumatic resin canals indicate the studied wood is most similar to *Sequoioxylon burejense*, but ray tracheids have not been found in the wood described here. We therefore assign the present specimen to *Sequoioxylon* cf. s. *burejense* noting its overall similarity with this existing species.

4.3 Palaeoenvironmental implications

One of the palaeobotanical methods for reconstructing Tertiary terrestrial climates is to identify the nearest living relatives (NLRs) of the elements in a given fossil flora and to apply the range of climate parameters of the NLRs to the fossil site (Royer *et al*., 2005; Dieter Uhl, 2006). The extant genus *Sequoia* has a long fossil record at the generic level, and the living *Sequoia* only includes a single species, *Sequoia sempervirens* (common name: Redwood). *S. sempervirens* is naturally distributed in the Northern California coastal forests eco-region of Northern California and Southern Oregon in the United States. Coast redwoods occupy a narrow strip of land approximately 750 km in length and 8−75 km in width along the Pacific coast of North America. The elevation range is mostly from 30−750 meters above sea level, occasionally down to 0 and up to 920 m (Farjon, 2005). S. *sempervirens* usually grows in mountains where precipitation from the incoming moisture off the ocean is greater. Redwood forests grow in a unique environment with heavy seasonal rains (2500 mm annually). Cool coastal air and fog drip keep this forest consistently damp year round. This forest community includes coast Douglas-fir, western hemlock, tanoak, Pacific madrone, and other trees, along with a wide variety of ferns, redwood sorrel, mosses and mushrooms (Earle, 2011).

The general vegetation through the section of the studied coal seam shows warm temperate deciduous forest cover with some subtropical elements based on palynology. The spore and pollen assemblage is represented by *Carya*, *Juglans*, *Pterocarya*, *Quercus* and *Liqudambar*, *Nyssa*, *Ilex*, Magnoliaceae, *Taxodium*, *Glyotostrobus* and *Sequoia* (Syabryaj, 1997). The leaf remains of *Taxodium dubium*, *Glyptostrobus europaeus* and *Sequoia langsdorfii* are also reported from the Ilitsa Suite (Iljinskaja, 1968). The studied wood further confirms the presence of *Sequoia* as an element of this forest community and indicates the climate of the fossil locality in the Late Pliocene had heavy seasonal rains and most likely fog drip from foliage.

In conclusion, this paper describes a new record of fossil wood with anatomy most similar to *Sequoia* from Pliocene aged coal deposits of the Gorbki brown coal field in the Transcarpathian region of the Ukraine. This wood represents an important contribution to the poorly understood vegetation that existed in the Late Pliocene period in this region. This fossil confirms that taxodiaceous conifers were a part of the swamp community under a prevailing warm temperate−subtropical climate regime.

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